

What determines the number of dominant species in forests?

HE Xing-bing • LIN Yong-hui • HAN Guo-min • TIAN Xing-jun

Received: 2009-09-24 Accepted: 2009-12-22
© Northeast Forestry University and Springer-Verlag Berlin Heidelberg 2010

Abstract: In this work, the difference in number of dominant species in a community on global scale and successional trajectories was analyzed based on the published data. We explained the reasons of these differences using a resource availability hypothesis, proposed in this work, that the distribution of available resource determined the pattern of community dominance. The results showed that on global scale the number of dominant species of community varied across latitudinal forest zone, namely from single-species dominance in boreal and temperate forest to multi-species codominance, even no dominant species in tropical forest. This was consistent with the pattern of resource distribution on global scale. Similarly, in successional trajectories, the number of dominant species gradually radiated from single-species dominance to multi-species codominance, even no dominant species in tropical forest. The changing available resources in trajectories were responsible for this difference. By contrary, a community was often dominated by single species in temperate or boreal forest. This was determined by the low available resource, especially low available water and temperature. In boreal forest, low temperature greatly reduced availability of water and nutrient, which were responsible for the single-species dominance. In addition, the conclusion that high available resources sustained low dominance of community might be deduced, based on the fact that the dominance of community declined with the increasing of species diversity. To sum up, the richer the available resources were, the lower the dominance of community was, and vice versa. The hypothesis that the

resource availability controlled the dominance of community could well elucidate the difference of community dominance on global and community scale.

Keywords: codominance; resource availability; single dominance

Introduction

The dominance of forest in the horizontal zonation, mainly including boreal forest, temperate forest and tropical forest, decreases gradually from dominance by single species to codominance by several species, even no dominant species. What does this dominance of forest result from? Does the dominance of forest change with habitat? According to Keel and Prance (1979), dominance increased as a function of stress, while Jacobs (1987) hold that in tropical forests dominance by single species often suggested the forest was destroyed before. Usually, the single-species dominated forest occurred in the early successional stage of tropical forest (Yu et al. 1994; Huang et al. 2002). However, disturbance may not be a sole reason for single species dominance (Swamy et al. 2000). Richards (1952) suggested that adverse climatic conditions also sometimes resulted in single species dominance. Actually, disturbance and climatic conditions only locally interpret the dominance. In boreal or temperate forest, climax community is dominated by single species intensively. Also the climatic conditions can't elucidate the essence of dominance because that although tropical forest has excellent moisture and temperature conditions, huge spatial structure, abundant organisms, and high biomass, the soil nutrient store is low (Ceccon et al. 2003), so the destruction of the forest and removal of the above-ground vegetation will permit the loss of the limited soil nutrient reserves by erosion and leaching, and on the adverse condition only one species can dominate community (Fang and Peng 1995). In order to explain dominance of forest community, we put forward available resource hypothesis that the dominance of forest community depends on available resource. We believe that to some extent the disturbance and climatic conditions control available resource (mainly including light, temperature, water, and soil nutrients) which is responsible for the difference of community dominance. The aim of this paper is: (1) to view the trend or difference of community dominance on different scale;

Foundation project: This paper was supported by Normal Projects of National Natural Science Foundation of China (30870419, 40971151), Project “948” of State Forestry Administration (2006-4-13), and Scientific Research Fund of Hunan Provincial Education Department (08C674).

The online version is available at <http://www.springerlink.com>

HE Xing-bing • HAN Guo-min • TIAN Xing-jun (✉)

School of Life Science, Nanjing University, Nanjing, 210093, P. R. China. Email: tianxj@nju.edu.cn

HE Xing-bing • LIN Yong-hui

Key Laboratory of Plant Resources Conservation and Utilization (Jishou University), College of Hunan Province, Jishou, 416000, P. R. China.

Responsible editor: Hu Yanbo

(2) to validate available resource hypothesis.

Materials and methods

Data collection

Data on community dominance are collected from former published literature. The relative important value (RIV) of a species may be a critical indicator to illustrate the importance of the species in the forests. In order to compare RIV from different researches, the references with the same RIV calculation equation ($RIV = \text{sum of (relative density} + \text{relative frequency} + \text{relative dominance}) \times 100 / 3$) were selected for analysis. RIV of first dominant species, which represents the codominance or single-dominance to a large degree, was selected for analyses.

Data analysis

Forest dominance trend or difference on global and community scale was analyzed. Pearson correlation and hierarchical cluster analyses were conducted to analyze the relationship between RIV of first dominant species and tree species number. Statistical significance for analyses was set at $p < 0.05$. The above analyses were obtained by the SPSS statistical software package version 15.0.

Results

Community dominance pattern in latitudinal forest zone

According to the former researches, in north hemisphere the dominance of climax community varies across the different forest zone. RIV of first dominant species in successional climax of community is approximately 5–20% in tropical forest (Swamy et al. 2000; La Torre-Cuadros and Islebe 2003; Ramanujam and Cyril 2003; Small et al. 2004), 30–50% in temperate forest (Cheng et al. 1999), and over 60% in boreal forest. In climax community of tropical forest, there is multi-species codominance or no prominent dominant species under rich resource conditions. In temperate forest single species dominance is often observed, but codominance is infrequent. The climax vegetation in boreal forest zone is mostly dominated by spruce and pine, and moreover the dominance of community is the most prominent among all forest zones (Jasinski and Angelstam 2002; Lehtonen et al. 2004).

Dominance pattern in successional communities

After disturbance such as over-logging and storm, the dominance of community varies with the proceeding of succession. In tropical forest, few tree species occur in the early stage of succession, and sometimes only one species can dominate the forest. After the primary forest being logged or burned, soil becomes dry and poor. *Pinus latheri*, which is a light-demanded pioneer species,

will adapt to this adverse environment and gradually develops to pure forest, which could last steady for 100 years (Huang et al. 2002). With the proceeding of succession, the single species dominance of early stage of successional trajectories will be replaced by two or more species and the RIV of first dominant species declines gradually. For example, in *Dacrydium pierrei-Xanthophyllum hainanense-Syzygium araiocladium* community, which is in the mid-stage of succession, *D. pierrei* retreats gradually from the dominant species group because of the poor regeneration ability, while the moderate-demanded species such as *X. hainanense*, *S. araiocladium*, and *Cryptocarya chinensis* will codominate the community (Yu et al. 1994). Across the successional trajectories the dominance of community in tropical forest declines gradually, from single species dominance to multi-species codominance, even no dominant species (Finegan 1996). However, in temperate or boreal forest the process of succession is simple and lacks of species replacement following disturbance (Carleton and Maycock 1978). Often the forest is dominated exclusively by pine or spruce in the successional trajectories (Harper et al. 2002; 2003).

Relationship between species diversity and RIV of first dominant species

1

Based on plenty of researches in all forest zones, we selected 60 groups of datum determined by the number of tree species and the RIV of first dominant species (Table 1). Correlation analysis (Table 1) shows that there is negatively significant correlation ($n=60$, $r=-0.517$, $p < 0.001$) between them. Peltzer et al. (2000) conformed from dominance-diversity curves that lower diversity in forest was in line with lower evenness. Cluster analysis (Fig. 1) shows that the 60 groups' data is obviously classified into four clusters based on RIV of first dominant species and tree species number. For example, the data with the lowest RIV of first dominant species and the most tree species number, including code 3, 39, 35 and 54, have merged into one cluster.

Discussion

On global scale

Along the latitudinal zone from equator to artic pole, the rainfall and quantity of heat decrease gradually. The annual precipitation is about 1 500–4 000 mm, 500–1 000 mm, and less than 500 mm in tropical forest zone, temperate zone, and boreal zone, respectively (Wirth et al. 2002). The mean annual air temperature also shows the same trend as rainfall, about 20–25°C in tropical forest, 5–15°C in temperate zone, and often below 0°C in boreal forest. Soils also are greatly important to plant regeneration and growth. The soil nutrient and organic matter in tropical forest are the lowest because of the fast turnover rate of soil nutrient and organic matter. Therefore, the soil is relatively poor in tropical forest, but soil nutrient can be fully assimilated to supply for the growth and regeneration of plant. By contrary, in boreal forest zone, extreme cold and a short summer growing season are its

predominant environmental features. Low air and soil temperature impose clear limits on the regeneration and growth of trees, and are an important determinant of the rate at which biological processes occur (Henttonen et al. 1986). Excess moisture and consequent oxygen-deficient and extreme low temperature conditions are a major cause of slow mineralization of nutrient and thick accumulation of organic matter in boreal forest (Prescott et al. 2000). So the available nutrient absorbed by plant in boreal forest is very low. This pattern of available resource on global scale determines the distribution of climax community dominance represented, to great extent, by the RIV of first dominant species of community from tropical forest to boreal forest, namely the dominance of climax community is more and more prominent

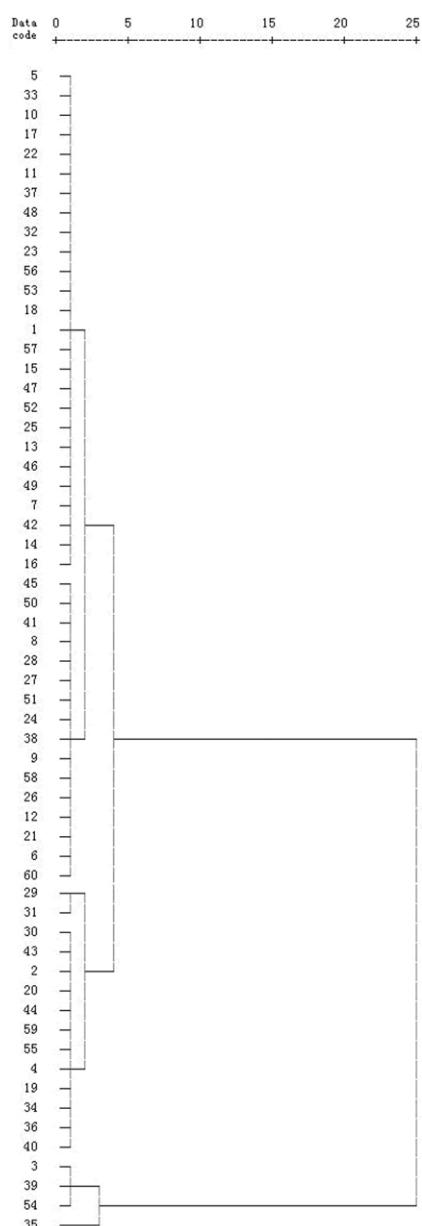


Fig. 1 Hierarchical cluster analysis for the 60 groups' data in Table 1.

Successional trajectories

Large and short-term disturbance such as over-logging, fire, flood, and storm, can remove the biomass aboveground and degrade the soil. In tropical forest, large disturbance such as extensive logging, extensive tree-fall by storm, flood, and fire, often occur. With the elimination of the plant biomass, firstly, disturbance can induce the degradation of habitat and the losing of topsoil and especially intensify the leanness of soil because of washing by high precipitation which is the dominant pathway for nutrient loss. And then directly hitting the bare ground surface by rainfall can disperse the soil structures into finer particles, which then clog the soil pores. Fire, which is a destructive calamity, can release most of mineral nutrients in the plant biomass for return to the soil, where they become readily available for plant growth. Burning also converts litter and humus of low pH to ash of higher pH which encourages nitrogen-fixing bacteria to produce more nitrogen and these processes improve the soil fertility, while this benefit may not last long. Most of the nutrients will soon be washed away by subsequent rains. Thus, the burning of vegetation will greatly reduce the availability of nutrients in the ecosystem and increase the incidence and intensity of flash floods as well as accelerating soil erosion and siltation. Moreover, disturbance can damage the soil fungal flora that help roots of plant species absorb nutrients from the soil and litter. Large disturbances greatly decrease resource availability in ecological communities (Davis and Moritz 2001). Low available resource, especially soil nutrient and water, can't favor the regeneration of most tree species, and only few tree species can adapt to this adverse habitat. Moreover, low available resource can increase competition among tree seedling or sapling, and then can induce the contabescence of tree species with low competitive ability. Thus, competition gives advantage to species differentiation, which makes one or several species dominate the community. For example, after intensive destruction the forest is often dominated by pine or beech for decades (Fang and Peng 1995). The development of community can improve itself resource availability. Along successional trajectories, pioneer species constantly add organic matter and nitrogen to soil and the ameliorated soil provides a suitable environment for later successional species of vegetation. A high rate of litterfall in restored forests helps restore soil by circulating more nutrients that, to great extent, tune up the regeneration of tree species (Lugo et al. 2004). Organic matter accumulation also alters the conditions in the root zone of the vegetation and influences the species composition. The development of community and litter accumulation can improve the light heterogeneity for seed germination and plant growth. Litter accumulation also can increase soil water which is necessary to tree seed germination and nutrient cycling. The resource availability gradually increases with the proceeding of succession. High nutrient availability can reduce the competitive ability of some plants. High nutrient and weak competitive ability give great chance to the codominance of multi-species. The temporal pattern of resource availability positively restricts community dominance from single species dominance to

codominance by several species along successional trajectories in tropical forest. Similarly, during retrogressive succession the community dominance becomes more and more conspicuous,

which is positively restricted by the declining resource availability, especially soil nutrient availability (Adema and Grootjans 2003; Bardgett 2001).

Table 1. Relative important value (RIV) of first dominant species (FDS) and the number of tree species (NTS) of community based on different researches

Data code	FDS	RIV of FDS	NTS	References	Data code	FDS	RIV of FDS	NTS	References
1	<i>Aglaia elaeagnoides</i>	25.80	15	Ramanujam and Cyril 2003	31	<i>Diospyros hainanensis</i>	9.27	87	Yang et al. 1994
2	<i>Agrostistachys meboldii</i>	21.60	53	Swamy et al. 2000	32	<i>Eurya nitida</i>	20.34	13	Ma et al. 2002
3	<i>Altingia obovata</i>	4.72	164	Fu and Feng 1995	33	<i>E. nitida</i>	19.42	18	Ma et al. 2002
4	<i>Beilschmiedia robusta</i>	21.27	69	Li et al. 2005	34	<i>Haematoxylum campechianum</i>	27.80	65	La Torre-Cuadros and Islebe 2003
5	<i>Castanea henryi</i>	18.89	18	Ma et al. 2002	35	<i>Heritiera parvifolia</i>	10.20	136	Yang et al. 1994
6	<i>Castanopsis carlesii</i>	62.12	36	Zhang et al. 1999	36	<i>Hopea parviflora</i>	34.60	74	Swamy et al. 2000
7	<i>C. carlesii</i>	33.10	17	Hong et al. 1999	37	<i>Lepisanthes tetraphylla</i>	17.40	18	Ramanujam and Cyril 2003
8	<i>C. carlesii</i>	45.90	8	Hong et al. 1999	38	<i>Lithocarpus glaber</i>	53.30	7	Hong et al. 1999
9	<i>C. carlesii</i>	53.00	10	He et al. 1998	39	<i>Mallotus hookerianus</i>	4.99	171	Fang et al. 2004
10	<i>C. carlesii</i>	20.38	19	Yan et al. 2002b	40	<i>Manilkara zapota</i>	10.10	68	La Torre-Cuadros and Islebe 2003
11	<i>C. eyrei</i>	22.30	17	Chen 1997	41	<i>Pinus latteri</i>	61.60	20	Huang et al. 2002
12	<i>C. eyrei</i>	48.90	31	Hong et al. 1999	42	<i>Phoebe bournei</i>	34.70	18	He et al. 1998
13	<i>C. eyrei</i>	35.40	11	He et al. 1998	43	<i>Podocarpus imbricatus</i>	22.52	42	Yang et al. 1994
14	<i>C. eyrei</i>	38.00	15	He et al. 1998	44	<i>P. imbricatus</i>	16.30	52	Yang et al. 1994
15	<i>C. eyrei</i>	29.60	16	He et al. 1998	45	<i>Quercus aliena</i> var. <i>acut-serrata</i>	65.90	13	Cheng et al. 1999
16	<i>C. fargesii</i>	37.70	17	Hong et al. 1999	46	<i>Q. glandulifera</i> var. <i>brevipetiolata</i>	36.50	9	Cheng et al. 1999
17	<i>C. fargesii</i>	22.15	20	Ma et al. 2002	47	<i>Q. glandulifera</i> var. <i>brevipetiolata</i>	31.90	14	Cheng et al. 1999
18	<i>C. fargesii</i>	8.16	25	Su et al. 1995	48	<i>Q. serrata</i>	15.64	19	Ma et al. 2002
19	<i>C. hystrix</i>	22.98	74	Li et al. 2005	49	<i>Q. serrata</i>	39.00	11	Cheng and Xiao 2000
20	<i>C. microcarpa</i>	19.30	57	Shi and Zhu 2003	50	<i>Q. variabilis</i>	63.25	15	Cheng et al. 1999
21	<i>C. platyacantha</i>	39.25	24	Yang et al. 1994	51	<i>Schima superba</i>	42.70	3	He et al. 1998
22	<i>C. platyacantha</i>	21.10	20	Bao et al. 2000	52	<i>Symplocos laurina</i>	32.19	11	Ma et al. 2002
23	<i>C. platyacantha</i>	13.90	22	Bao et al. 2000	53	<i>S. sumuntia</i>	11.80	20	Yan et al. 2002a
24	<i>C. tibetana</i>	52.80	6	He et al. 1998	54	<i>Syzygium araiocladium</i>	11.40	192	Yu et al. 1994
25	<i>Cunninghamia lanceolata</i>	29.61	8	Ma et al. 2002	55	<i>Terminalia paniculata</i>	33.30	48	Swamy et al. 2000
26	<i>C. lanceolata</i>	51.22	17	Ma et al. 2002	56	<i>Ternstroemia gymnanthera</i>	13.10	22	He et al. 1998
27	<i>C. lanceolata</i>	39.22	5	Ma et al. 2002	57	<i>Ulmus lamellosa</i>	26.60	12	Bi et al. 2003
28	<i>Cyclobalanopsis chungii</i>	48.00	8	Hong et al. 1999	58	<i>U. lamellosa</i>	58.70	6	Bi et al. 2003
29	<i>Dacrydium pierrei</i>	16.99	93	Yang et al. 1994	59	<i>Vatica astrotriloba</i>	19.17	62	Yang et al. 1994
30	<i>D. pierrei</i>	15.10	45	Yang et al. 1994	60	<i>V. mangachapoi</i>	49.89	44	Lan et al. 2007

Note: The area of community selected from former published literature \geq community minimal area.

The long-term and standing disturbance also can seriously destroy vegetation and topsoil, and then the soil nutrient, which is the limiting factor for plant growth in tropical forest, can't be recruited. These disturbances will lead to the changes of local forest community structure. The research of Ramanujam and Cyril (2003) indicated that the dominance of sacred groves community in anthropogenic stands were more prominent than that in natural forest. Swamy et al. (2000) also reported that repeated burning and other associated disturbances altered the course of succession by giving an advantage to certain species over others such as *Terminalia paniculata* which was single dominant species in its community.

Plant growth is strongly constrained by temperature and precipitation. In temperate or boreal forest, low precipitation and

temperature are major limiting factors for plant growth across the successional trajectories, and the available resource is still poor. Water availability is important for shaping forest structure and composition (Bugmann 2001). Syrjänen et al. (1994) reported that dry sites in natural boreal forest were almost exclusively occupied by *Pinus sylvestris* while on moist sites *Betula* sp. and *Populus tremula* codominated. Low available resource increases the competition, and single dominance of species mainly results from this competitive displacement of other tree species. Only in site with rich resource, there is codominance by two species before succession climax. Similarly, low temperature limits the temporal distribution of tree species on seasonal scale, so a few species can grow under low temperature. Low temperature limits absorbance of water and nutrient across the successional trajec-

tories, so single species often dominates the community, especially in boreal forest. In natural communities soil conditions may determine species composition. Nitrogen is a limiting resource in many temperate forests and nitrogen-fixing plants are usually limited to the early stages of post-disturbance succession. In early stage, the growth and metabolism of nitrogen-fixing plant are very slow, and the organic and inorganic nitrogen in soil are low. Thus, slow nitrogen accumulation limits plant regeneration. Therefore, the single-species dominant community in temperate forests is widely distributed. Regardless that the habitat is dominated by one species or co-dominated by two species in early stage of succession, succession will converge to single species dominance in temperate or boreal forest (Embong 1998).

Deduction from community dominance and species diversity

Low nutrient availability can in part result in low productivity. Resource availability and distribution are important determinants of local plant species diversity (Huston 1994). It is well known that high available resource can sustain high diversity. Based on the fact that the dominance of community declines with the increasing of species diversity on global or successional scale, we can deduce that high available resource may make the dominance of community decline, and vice versa.

Conclusion

Both the climatic conditions on the global scale and the disturbance on the local scale can not perfectly explain the essence of dominance. All the difference of dominance of community can be well elucidated by the difference of available resources on the fine scale, namely the resource availability limits the dominance of community. The richer the available resources are, the lower the dominance of community is. The dominance of different community is constrained by different single resource or the combination of several resources. The growth of single species is constrained by the ability of the species within community to acquire resources. Which species to be dominant also depends on the bio-ecological characteristics (such as reproductive ability, pollination ways, seed diffusion ways, maximal height, survival ability of seed and seedling, etc.) and some physi-ecological characteristics, including light-demand, shade-tolerance, low-temperature-tolerance, drought-tolerance, leanness-tolerance, high photosynthesis rate, etc. Sporadically, some stochastic events also can influence the dominance of species. In tropical forest, the member of the dominant species group in climax community isn't unchangeable, even if in the same forest type of similar habitat. The floristic composition of dominant species group can be slightly changed due to certain stochastic events. But the number of species in the dominant species group is still positively constrained by the resource availability. In temperate or boreal forest, the structure and composition are influenced less by chance, but more by competition. The community is intensively dominated by single and relatively fixed species (such as pine, spruce and beech, etc) under poor available resource (Na-

kashizuka 2001). To sum up, the richer the available resources are, the lower the dominance of community is, and vice versa.

References

- Adema EB, Grootjans AP. 2003. Possible positive-feedback mechanisms: plant change abiotic soil parameters in wet calcareous dune slacks. *Plant Ecology*, **167**: 141–149.
- Bao Weikai, Liu Zhaoguang, Liu Chaolu, Yuan Yafu, Wang Zewei. 2000. Comparison to floristic diversity of the primary and secondary humid evergreen broad-leaved forest in Wawushan National forest park of the South-western China. *Acta Botanica Yunnanica*, **22**: 408–418. (in Chinese)
- Bardgett RD. 2001. *Below-ground primary succession: a case study of the Cooloola dune system, Queensland (Grant Reports-SEPG1891)*. British Ecological Society.
- Bi Runcheng, Chen Lifang, Li Peiyu. 2003. Study on *Ulmus lamellose* community characteristics and species diversity in the south of Shanxi. *Journal of Wuhan Botanical Research*, **21**: 109–116. (in Chinese)
- Bugmann H. 2001. A comparative analysis of forest dynamics in the Swiss Alps and the Colorado Front Range. *Forest Ecology and Management*, **145**: 43–55.
- Carleton TJ, Maycock PF. 1978. Dynamics of the boreal forest south of James Bay. *Canadian Journal of Botany*, **56**: 1157–1173.
- Ceccon E, Huante P, Campo J. 2003. Effects of nitrogen and phosphorus fertilization on the survival and recruitment of seedlings of dominant tree species in two abandoned tropical dry forests in Yucatán, Mexico. *Forest Ecology and Management*, **182**: 387–402.
- Chen Qingquan. 1997. Study on feature of *Castanopsis eyrei* forest. *Journal of Fujian College Forestry*, **17**: 88–91. (in Chinese)
- Cheng Ruimei, Jiang Youxu, Xiao Wenfa, Liu Yucui. 1999. Community characteristics of *Quercus aliena* var. *acuteserrata* forest in Baotianman, Henan Province. *Chinese Journal Ecology*, **18**: 25–30. (in Chinese)
- Cheng Ruimei, Xiao Wenfa. 2000. A study on *Quercus serrata* community characteristics in Baotianman area, Henan Province. *Scientia Silvae Sinicae*, **36**: 21–25. (in Chinese)
- Davis FW, Moritz M. 2001. Mechanisms of disturbance. In S.A. Levin (Ed.), *Encyclopedia of Biodiversity*, vol. 2. San Diego: Academic Press, pp. 153–160.
- Embong J. 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, **106**: 83–95.
- Fang Jingyun, Li Yide, Zhu Biao, Liu Guohua, Zhou Guangyi. 2004. Community structures and species richness in the montane rain forest of Jianfengling, Hainan Island, China. *Biodiversity Science*, **12**: 29–43. (in Chinese)
- Fang Wei, Peng Shaolin. 1995. Changes of tree species in the succession process of *Pinus massoniana* community in Dinghushan, Guangdong, P. R. China. *Journal of Tropical and Subtropical Botany*, **3**: 30–37. (in Chinese)
- Finegan B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trees*, **11**: 119–124.
- Fu Guoai, Feng Shaoxin. 1995. The vertical distribution and characteristics of forest of Wuzhishan, Hainan. *Guizhou Forestry*, **15**: 57–69. (in Chinese)
- Harper KA, Bergeron Y, Gauthier S, Drapeau P. 2002. Structural development of black spruce forests following fire in Abitibi, Quebec: a landscape scale investigation. *Silva Fennica*, **36**: 249–263.

- Harper K, Boudreault C, De Grandpré L, Drapeau P, Gauthier S, Bergeron Y. 2003. Structure, composition and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. *Environmental Review*, **11**: 79–98.
- He Jinsheng, Chen Weilie, Xie Zongqiang. 1998. Types of the evergreen broadleaf forest and their community species diversity in Longqishan nature reserve, Fujian Province. *Chinese Journal of Ecology*, **17**: 1–6. (in Chinese)
- Henttonen H, Kanninen M, Nygren M, Ojansuu R. 1986. The maturation of Scots pine seeds in relation to temperature climate in northern Finland. *Scandinavian Journal of Forest Research*, **14**: 617–622.
- Hong Wei, Lin Chenglai, Wu Chengzhen, He Dongjin, Chen Kun. 1999. Research on species diversity of evergreen broad-leaved shelter-forests in Jianxi River valley, Fujian. *Chinese Biodiversity*, **7**: 208–213. (in Chinese)
- Huang Qinlin, Chen Yongfu, Yang Xiuren. 2002. Study on the characters of tree stratum of *Pinus Latteri* forest in Bawangling Forestry Area of Hainan Province. *Forest Research*, **15**: 741–745. (in Chinese)
- Huston MA. 1994. *Biological diversity: The co-existence of species on changing landscapes*. Cambridge: Cambridge University Press, p.681.
- Jacobs M. 1987. *The tropical rain forest*. New York: Springer-Verlag.
- Jasinski K, Angelstam P. 2002. Long-term differences in the dynamics within a natural forest landscape – consequences for management. *Forest Ecology and Management*, **161**: 1–11.
- Keel SHK, Prance GT. 1979. Studies of the vegetation of a white-sand black-water igapo (Rio Negro, Brazil). *Acta Amazonica*, **9**: 645–655.
- La Torre-Cuadros MA, Islebe GA. 2003. Traditional ecological knowledge and use of vegetation in southeastern Mexico: a case study from Solferino, Quintana Roo. *Biodiversity and Conservation*, **12**: 2455–2476.
- Lan Guoyu, Chen Wei, Zhou Xiaofei. 2007. Communitive characteristics of *Vatica mangachapoi* forest of Bawangling in Hainan, South China. *Acta Bot Boreal-Occident Sin*, **27**: 1861–1868. (in Chinese)
- Lehtonen A, Mäkipää R, Heikkilä J, Sievänen R, Liski J. 2004. Biomass expansion factors (BEFs) for Scots pine, Norway spruce and birch according to stand age for boreal forests. *Forest Ecology and Management*, **188**: 211–224.
- Li Zongshan, Tang Jianwei, Zheng Zheng. 2005. Analysis on the coenological characteristics of tropical montane rain forest in Lancang, South Yunnan. *Guizhou*, **25**: 206–214.
- Lugo AE, Silver WL, Colón SM. 2004. Biomass and nutrient dynamics of restored neotropical forests. *Water, Air, and Soil Pollution: Focus*, **4**: 731–746.
- Ma Danwei, Zhang Guo, Wang Yuehua, Wang Daomuo. 2002. Studies on species diversity of forest vegetation on Qingcheng Mountain. *Journal of Sichuan University*, **39**: 115–123. (in Chinese)
- Nakashizuka T. 2001. Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology & Evolution*, **16**: 205–210.
- Peltzer DA, Bast ML, Wilson SD, Gerry AK. 2000. Plant diversity and tree responses following contrasting disturbances in boreal forest. *Forest Ecology and Management*, **127**: 191–203.
- Prescott CE, Maynard DG, Laiho R. 2000. Humus in northern forests: friend or foe? *Forest Ecology and Management*, **133**: 23–26.
- Ramanujam MP, Cyril KPK. 2003. Woody species diversity of four sacred groves in the Pondicherry region of South India. *Biodiversity and Conservation*, **12**: 289–299.
- Richards PW. 1952. *The Tropical Rain Forest*. London: Cambridge University Press, p102-108.
- Shi Jipu, Zhu Hua. 2003. A community ecology study on the monsoonal evergreen broad-leaved forest in tropical montane of Xishuangbanna. *Acta Botanica Yunnanica*, **25**: 513–520. (in Chinese)
- Small A, Martin GT, Kitching RL, Wong KM. 2004. Contribution of tree species to the biodiversity of a 1 ha Old World rainforest in Brunei, Borneo. *Biodiversity and Conservation*, **13**: 2067–2088.
- Su Zhiyao, Chen Beiguang, Gu Yankun. 1995. Floristic composition and structural characteristics of forest communities in Babaoshan Nature Reserve, North Guangdong. *Guizhou*, **15**: 124–130. (in Chinese)
- Swamy PS, Sundarapandian SM, Chandrasekar P, Chandrasekaran S. 2000. Plant species diversity and tree population structure of a humid tropical forest in Tamil Nadu, India. *Biodiversity and Conservation*, **9**: 1643–1669.
- Syrjänen K, Kalliola R, Puolasmaa A. 1994. Landscape structure and forest dynamics in sub-continental Russian European taiga. *Annales Zoologici Fennici*, **31**: 19–34.
- Wirth C, Schulze ED, Lüker B, Grigoriev S, Siry M, Hardes G. 2002. Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant and Soil*, **242**: 41–63.
- Yan Shujun, Hong Wei, Wu Chengzhen, Bi Xiaoli, Fan Hailan, Chen Rui. 2002a. Height niche of main tree species of gaps in mid-subtropical evergreen broad-leaved forest in Wannmulin of Fujian. *Chinese Journal of Applied Environmental Biology*, **8**: 578–582. (in Chinese)
- Yan Shujun, Hong Wei, Wu Chengzhen, Bi Xiaoli, Lan Bin. 2002b. The structure and distribution pattern of dominant populations in *Castanopsis carlesii* community. *Journal of Tropical and Subtropical Botany*, **10**: 15–21. (in Chinese)
- Yang Yichuan, Zhuang Ping, Li Xirong. 1994. Ecological studies on the forest community of *Castanopsis platyacantha-Schima sinensis* on Emei Mountain. *Acta Phytocologica Sinica*, **18**: 105–120. (in Chinese)
- Yu Shixiao, Zhang Hongda, Wang Bosun. 1994. The tropical montane rain forest of Bawangling Nature Reserve, Hainan Island II. Quantitative analyses of the community structure. *Ecological Science*, **1**: 21–31. (in Chinese)
- Zhang Muming, Chen Beiguang, Shen Xiaoming. 1999. Species diversity of the *Castanopsis carlesii* forest at Luoba, Shixing, Guangdong. *University Journal of South China Agricultural University*, **20**: 98–102. (in Chinese)